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ORIGINAL PAPER

First documentation of scent-marking behaviors in striped skunks (*Mephitis mephitis*)

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Abstract

Communication behaviors play a critical role in both an individual's fitness as well as the viability of populations. Solitary animals use chemical communication (i.e., scent marking) to locate mates and defend their territory to increase their own fitness. Previous research has suggested that striped skunks (*Mephitis mephitis*) do not perform scent-marking behaviors, despite being best known for using odor as chemical defense. We used video camera traps to document behaviors exhibited by striped skunks at a remote site in coastal California between January 2012 and April 2015. Our camera traps captured a total of 71 visits by striped skunks, the majority of which (73%) included a striped skunk exhibiting scent-marking behaviors. Overall, we documented 8 different scent-marking behaviors. The most frequent behaviors we documented were cheek rubbing (45.1%), investigating (40.8%), and claw marking (35.2%). The behaviors exhibited for the longest durations on average were grooming ($\bar{x}$ = 34. 4 s) and investigating ($\bar{x}$ = 21.2 s). Although previous research suggested that striped skunks do not scent mark, we documented that at least some populations do and our findings suggest that certain sites are used for communication via scent marking. Our study further highlights how camera traps allow researchers to discover previously undocumented animal behaviors.

Keywords Camera trap · Chemical communication · Communication · *Mephitis mephitis* · Novel behaviors · Scent marking · Striped skunk

Introduction

Intraspecific communication via physical and chemical cues (i.e., scent marks) plays a vital role in communication among animals by affecting individual fitness and regulating population structure and distribution (Allen et al. 2015a; Wooldridge et al. 2019). Scent marking is an inexpensive form of chemical communication that allows individuals to send signals indirectly to other individuals (Gosling and Roberts 2001; Steiger et al. 2011; Krofel et al. 2017; Vogt et al. 2014). Scent marking is necessary for solitary species to communicate, unlike animal communities that exhibit gregariousness and cooperative societies where males and females are continually interacting (Russell et al. 2003). For example, solitary carnivores with large home ranges use scent marking to advertise their location for both potential mates (Mellen 1993; Vogt et al. 2014; Allen et al. 2015a) and territorial competitors (Ralls 1971; Bailey 1974; Gosling and Roberts 2001; Allen et al. 2016a). A multitude of scent-marking behaviors have been documented in solitary carnivores, including urine spraying, fecal deposition, body rubbing, and claw marking (Allen et al. 2014; Vogt et al. 2014; Allen et al. 2016b; Wooldridge et al. 2019). Behaviors such as claw marking, biting, and scraping are likely visual cues that help conspecifics locate scent marks and as such fall under the same umbrella term of scent marking (Taylor et al. 2015; Vogt et al. 2014; Allen et al. 2016b). Effects of communication behaviors can ripple through entire communities, making it important to

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understand the specific scent-marking behaviors of solitary carnivores and why they perform them.

Striped skunks (*Mephitis mephitis*) are solitary, non-territorial carnivores (Lariviere and Messier 1998a), but it is unknown how they communicate to find and select mates. Striped skunks are one of the best known examples of animals who use odor as a chemical defense (Fisher and Stankowich 2018). Their scent glands, along with their aposematic coloring (black and white coloring that is used to signal warning), are primarily used for defense (Nams 1991; Lariviere and Messier 1996). Despite being best known for their olfactory cues, striped skunks are thought to not scent mark based on extensive direct observations (Nams 1991; Lariviere and Messier 1996; Lariviere and Messier 1998b). This may be because striped skunks, like other aposematic animals, have short range sensory abilities (Nams 1991; Lariviere and Messier 1996), and may not be able to detect the presence of other individuals unless in close proximity (Lariviere and Messier 1996). Home ranges of striped skunks overlap both inter- and intra-sexually, but apparently have no defense or other mechanisms to establish a territory (Verts 1967; Lariviere and Messier 1996; Lariviere and Messier 1998b). This includes not marking their burrows (Lariviere and Messier 1996), although the strong natural body odor of skunks may be sufficient to communicate occupancy of dens (Lariviere and Messier 1996). Despite being considered solitary carnivores, however, multiple female striped skunks have been documented sharing the same den or resting sites during natal season (Lariviere and Messier 1998b). How striped skunks communicate intraspecifically is a missing link in their behavioral ecology.

We investigated striped skunk communication behaviors at a location in coastal California using video camera traps. Our objective was to document communication and scent-marking behaviors and to determine the frequency and duration of these behaviors. Based on studies of other cryptic carnivores with unknown communication behaviors (e.g., Allen et al. 2016b), we expected striped skunks to exhibit some communication behaviors more frequently than others. Specifically, we expected behaviors using urine and feces marking to be a predominate form of communication behaviors displayed (e.g., Vogt et al. 2014; Allen et al. 2015b). We also expected communication behaviors to be exhibited most frequently by striped skunks during the breeding season (e.g., Vogt et al. 2014; Taylor et al. 2015).

Materials and methods

Study area

We conducted our study at a single site in the Santa Cruz Mountains of California, in the Soquel Demonstration Forest in Santa Cruz County. Elevations range from sea level to 1155 m, with vegetative communities changing with elevation and distance to the coast. Vegetative communities are primarily forested at high elevations, including redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*), or mixed hardwoods. Coastal areas and lower elevations on the east side of the Santa Cruz Mountains are primarily shrubs and grasslands. The climate is Mediterranean with hot, dry summers and mild, wet winters. Annual daily high temperatures ranged from 15.5–24.4 °C and annual precipitation varied from 58 cm to 121 cm throughout the mountain range.

Field methods

As part of a larger project studying puma (*Puma concolor*) ecology and behavior, we documented 299 puma scent marking areas, called "community scrapes" (Allen et al. 2015a; Allen et al. 2016a). We set up video camera traps (Bushnell Trophy Cam, Overland Park, KS) at 45 community scrapes from 2011 to 2015 and programmed the cameras to record a 60 s video at each trigger with a 1 s refractory period. All carnivore species found in the study area have been documented visiting the community scrapes (Allen et al. 2015b). For the purposes of this study, we focused on one site in the Soquel Demonstration Forest where striped skunks exhibited scent-marking behavior. For each visit by a striped skunk, we documented the date, time, and duration of visit, and created an ethogram of the behaviors we observed in the videos (Table 1).

Statistical analyses

We used program R version 3.6.3 (R Core Team 2016) for our statistical analyses, and in each statistical test, we considered $p < 0.05$ to be statistically significant. To reduce pseudoreplication, we considered videos taken less than 5 min apart to be the same visit (based on natural breaks in the data; Wang et al. 2015) and combined the behaviors and durations of behaviors in each visit into one value.

We first calculated summary statistics, including the number of behaviors exhibited, the days between visits, and a standardized monthly visitation rate (calculated as the number of visits divided by the number of monitoring days and multiplied by 100). To determine if any behaviors were displayed significantly more frequently than others, we used a z test for proportions (Sokal and Rohlf 2012). Across a series of tests, we used the number of visits where each behavior was exhibited as our variables. To determine if any behaviors were exhibited for longer durations of time than others, we used a two-tailed t test (Sokal and Rohlf 2012). We first tested for normality with Shapiro-Wilk tests (Sokal and Rohlf 2012), and then used the number of seconds each behavior was displayed as our variables across the series of tests.

Table 1 Ethogram of possible marking behaviors exhibited by striped skunks, captured with camera traps, from 2012 to 2015

Behavior	Description
Biting	The skunk's teeth are in contact with the fern and tall grass, using the teeth to actively remove grass and sink into the fern.
Body rubbing	The skunk rubs its stomach and lower sides against the fern and mound of dirt.
Cheek rubbing	The skunk rubs the sides of its face down to its neck against either side of the fern and mound of dirt.
Claw marking	The skunk's claws scrape against the fern and mound.
Grooming	The skunk uses its mouth and claws to remove foreign bodies and objects from its fur by scratching or biting them off, typically done immediately after scent marking.
Investigating	The skunk surveys the fern and surrounding area by sniffing and moving slowly around the site, frequently pausing around the mound of dirt.
Rolling	The skunk turns over onto its back with its paws pointed up, then turns over back onto its feet in a 360-degree roll.
Shaking	The skunk shakes its body by moving from side to side rapidly, head to tail, while standing.

Results

Over the duration of the study, we documented 71 visits of striped skunks at the site. During 73.2% of the visits (n = 52) striped skunks exhibited at least one of the eight marking behaviors (Table 1). We also documented other non-scent-marking behaviors at the site, including defensive rearing on 5 visits (mean duration = 2.8 s), digging on 8 visits (mean duration = 14.1 s), and foraging on 2 visits (mean duration = 31.5 s). On average, the days between visits by a striped skunk were 13.62 days (± 3.21 SE, range 0.02-141.03). Striped skunks tended to visit before sunrise, with 68% (n = 49) of the documented visit being in the morning with an average time of 4:47 AM. We documented visits during every month of the year, but visitation rates were most frequent from December through May, with a peak in January (Fig. 1).

Our most frequently displayed behaviors were cheek rubbing (45.1%) and investigating (40.8%; Fig. 2), which were displayed significantly more frequently than body rubbing (23.9%, $z \geq 2.2$, $p \leq 0.03$), grooming (12.7%, $z \geq 3.8$, $p < 0.001$), biting (7.0%, $z \geq 4.7$, $p < 0.0001$), and rolling (4.2%, $z \geq 5.2$, $p < 0.0001$). Our next most frequently displayed behaviors were claw marking (35.2%) and shaking (31.0%), which were displayed significantly more frequently than grooming (12.7%, $z \geq 2.6$, $p < 0.01$), biting ($z \geq 3.6$, $p < 0.0001$), rolling ($z \geq 4.2$, $p < 0.0001$). Body rubbing was also more frequently displayed than biting ($z = 2.8$, $p = 0.005$) and rolling ($z = 3.4$, $p = 0.0007$).

The behavior displayed for the longest durations (Fig. 3) was grooming ($\bar{x}$ = 34. 4 s), significantly longer than biting ($\bar{x}$ = 13.2 s, $t = 2.23$, $p = 0.04$), claw marking ($\bar{x}$ = 5.2 s, $t = 7.08$, $p < 0.0001$), cheek rubbing ($\bar{x}$ = 9.9 s, $t = 5.69$, $p < 0.0001$), body rubbing ($\bar{x}$ = 4.3 s, $t = 6.31$, $p < 0.0001$), rolling ($\bar{x}$ = 3.0 s, $t = 2.70$, $p = 0.02$), and shaking ($\bar{x}$ = 1.8 s, $t = 8.03$, $p < 0.0001$). The behavior with the second longest duration was investigating ($\bar{x}$ = 21.2 s), which was displayed longer than claw marking ($t = 4.05$, $p = 0.0002$), cheek rubbing ($t = 3.07$, $p = 0.003$), body rubbing ($t = 3.57$, $p = 0.0009$), and shaking ($t = 4.7$, $p < 0.0001$). Biting and cheek rubbing ($\bar{x}$ = 21.2 s) were displayed for significantly longer durations than body rubbing ($t \geq 2.8$, $p < 0.01$), claw marking ($t \geq 2.6$, $p < 0.01$), and shaking ($t \geq 4.8$, $p < 0.0001$). Claw marking was also displayed for significantly longer than shaking ($t = 3.36$, $p = 0.002$).

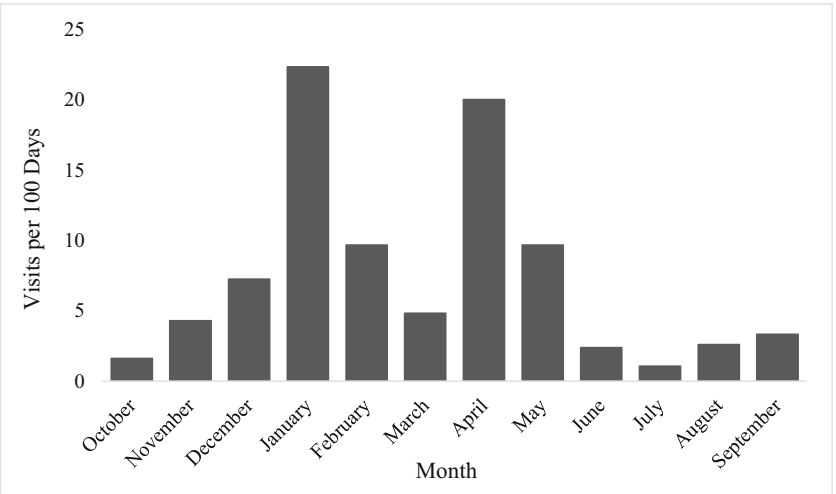

Fig. 1 Visit rate per month of striped skunks at a scent-marking site in central California

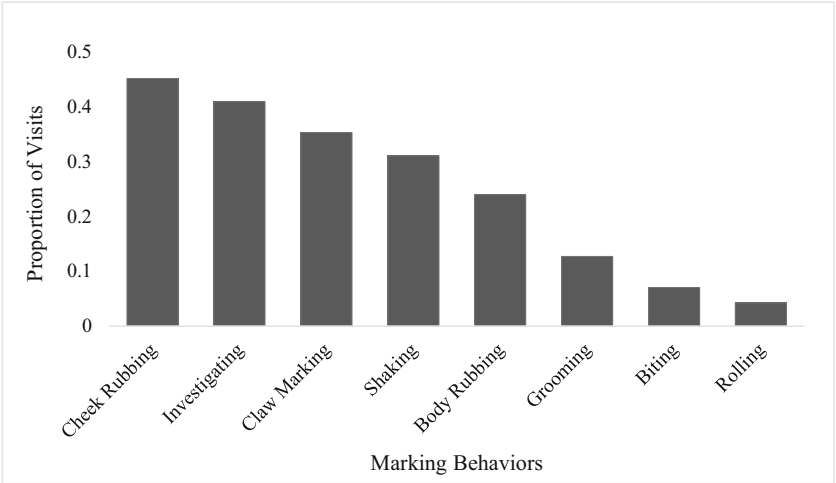

Fig. 2 Proportion of visits in which each scent-marking behavior was displayed

Discussion

Our study provides the first documentation of communication behaviors by striped skunks and contradicts previous studies suggesting that striped skunks do not scent mark (Nams 1991; Lariviere and Messier 1996; Lariviere and Messier 1998a). We documented a variety of behaviors by striped skunks that are associated with scent-marking behaviors in other solitary carnivores (i.e., cheek and body rubbing, claw marking by bears; Taylor et al. 2015; and cheek rubbing, claw marking, and rolling exhibited by felids; Allen et al. 2016b), although in skunks behaviors such as biting and claw marking are likely more visual cues associated with scent marking than scent marks themselves. Because striped skunks use behaviors similar to other solitary carnivores, it is most plausible that they use these behaviors for the same reason (e.g., scent marking for conspecifics). The use of camera traps has allowed the documentation of scent marking and other previously undocumented behaviors (Smith et al. 1989; Allen et al. 2015b; Vogt et al. 2014), including scent marking in species that were thought to not use scent-marking behaviors (Allen et al. 2016b). Despite previous studies that concluded otherwise, our evidence with video camera traps shows that striped skunks do scent mark.

The most frequent communication behaviors striped skunks exhibited were cheek rubbing, investigating, and claw marking (Fig. 2), while grooming and investigating had the longest mean durations. Investigating was apparently an important behavior (among the most frequent and of the longest duration), and skunks often initially investigated the surrounding location and the primary marking site before performing other scent-marking behaviors. Grooming and shaking typically occurred after other marking behaviors, such as cheek and body rubbing. Interestingly, while shaking had one of the shortest durations on average, it was a frequent behavior. Striped skunks may use cheek rubbing and claw marking

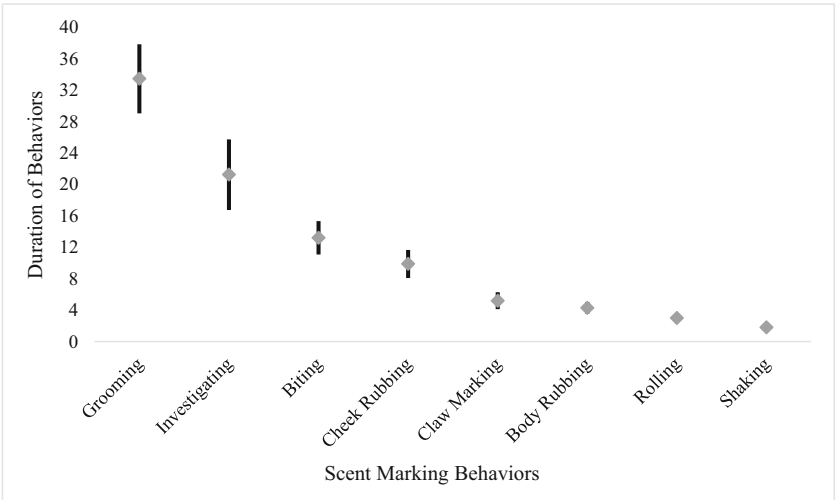

Fig. 3 Duration (in seconds) of scent-marking behaviors observed in striped skunks

more than other marking behaviors because their individual scent can hold longer compared to biting or full-body-marking behaviors. We also noted other behaviors that were not associated with scent marking, including defensive rearing and foraging. Previous studies that claimed striped skunks do not scent mark may have considered scent marking to only consist of urine spraying and failed to document other scent-marking behaviors. Despite our hypotheses, we did not note any evidence of urine or feces marking by striped skunks, although these may have occurred, and we were unable to discern from the videos recorded by the camera traps.

Striped skunks visited the marking site most frequently from December through February, and most marking behaviors took place in the early morning. This peak in visitation likely correlates to their breeding season in central California, which is between January and early March (Baldwin 2015). Animals likely select locations for marking that are most likely to be found by conspecifics (Allen et al. 2017a). The area that got the most attention from the striped skunks was a small root ball of a fern. The fern was where most of the claw marking, cheek rubbing, and biting took place. While we are unsure as to why the area became a well-used marking location, the frequency of visits makes it clear that it was a specific marking area of interest to striped skunks. The site could also be important because of interspecific marking (e.g., Allen et al. 2017b), although we did not document pumas marking on the root ball. We were able to document one occurrence of a striped skunk and a bobcat visiting the fern ball within minutes of each other, but with only one documentation, we were unable to discern a pattern. While we monitored many other sites in the same study area, this was the only site where we documented scent marking by striped skunks. Further research, specifically with camera traps, can be performed to determine why and where striped skunks scent mark, and what effects it has on intra- and inter-species relationships.

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